CYTOPLASMIC INHERITANCE OF PLASTIDS IN *IMPATIENS SULTANII* HOOK, F., *PETUNIA VIOLACEA* LINDL. AND *CHOLROPHYTUM ELATUM* R. BR.[1]

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INTRODUCTION

The inheritance and mode of chlorophyll distribution in variegated plants have long attracted the attention of botanists. It is probable that most variegated varieties of plant species, domesticated and wild, are somatic, mutant individuals which appear as chimeras (Blaydes, 1953). Many of these may be propagated vegetatively and persist indefinitely through the aid of man. However, the understanding of the processes involved in the structure and inheritance of leaf variegation is still far from complete.

A favorable condition for the study of chlorophyll inheritance is found in plants where one or more shoots are completely albino. Such shoots are incapable of independent existence, except when under special cultural methods, and may be found as mutants or somatic segregates on green or variegated plants (Blaydes, 1953). The most frequent occurrence of such albino mutants is found in periclinally, mericlinally and sectorially variegated plants. Since flowers on albino shoots are frequently unable to produce seed normally, mericlinal, periclinal, or sectorial chimeras are generally used for genetical experiments. As the reproductive cells are derived from the sub-epidermal layer of the shoot, the second layer of the shoot apex must be regularly albino if the genetic data from crosses in such plants are to be relied upon. Sectorially variegated plants in which the histogenic tissues are constantly rearranging are not reliable for genetic studies on variegation. Periclinally variegated plants, on the other hand, are histogenically much more stable and are satisfactory material for such investigations. A large number of periclinally variegated plants in which histogenic layers, L–II in Dicots, or L–II and L–III in Monocots (Dermen, 1947; Imai, 1935), are albino is available in nature. The present study has been carried out upon periclinally variegated plants of *Chlorophytum elatum* R. Br. and *Impatiens sultanii* Hook. f.

Types of Plastid Inheritance

Mendelian.—In a large number of plants albino seedlings appear in the progeny of the heterozygous parent which carries the recessive albino gene. Albino seedlings which die soon after germination have been found to segregate in a simple Mendelian ratio in *Antirrhinum latifolium* and *Melandrium album* (Baur, 1910), *Zea mays* (Lindstrom, 1918; Beadle, 1929), *Hordeum distichum* (Kiessling, 1918), *Phaseolus vulgaris* (Tjebbes and Kooiman, 1919), *Eleusine indica, Sorghum* species, *Eleusine coracana, Pennisetum typhoides, Setaria italica* and *Paspalum scrobiculatum* (Rangaswamy Ayyangar *et al.*, 1931, 1932, 1935, 1936), *Oryza sativa* (Ramiah *et al.*, 1935), *Coleus blumei* (Rife, 1948) and others. Mendelian segregations of pale green or yellowish green seedlings have been reported in *Urtica pilulifera* (Correns, 1909), *Ipomoea hederacea* (Mizazawa, 1918), *Mirabilis jalapa xantha* (Correns, 1918), *Zea mays* (Lindstrom, 1918), *Nicotiana rustica* (Allard, 1919),

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Pelargonium species (Chittenden, 1926), *Oryza sativa* (Ramiah *et al.*, 1935), *Secale cereale* and *Eleusine coracana* (Ramiah *et al.*, 1935), *Sorghum* species, *Setaria italica* and *Paspalum scrobiculatum* (Rangaswamy Ayyangar *et al.*, 1935, 1941), *Hordeum vulgare* (Smith, 1951), *Allium cepa* (Yarnell, 1954), *Coleus blumei* (Boye and Rife, 1938) and others. Various types of chlorophyll variegations have also been shown to segregate as simple Mendelian recessives in *Lunaria* (Correns, 1909), *Aquilegia vulgaris* (Baur, 1918), *Pisum arvense* (*P. sativum*) (Rajanus, 1918), *Capsella bursa-pastoris* and *Arabis albida* (Correns, 1919), *Hordeum vulgare* (Imai, 1936), *Oryza sativa* (Jodon, 1940), *Coleus blumei* (Pandey, unpublished) and others. However, Kempton (1924) found albinism dominant to green in maize. Inheritance of variegation governed by nuclear factors is also found in *Antirrhinum* sp. (Baur, 1910), *Zea mays* (Beadle, 1929), *Urtica peraurea*, *Mirabilis jalapa variegata*, *Pelargonium chlorina* (cited by Sansome and Philp, 1939) and other species.

Non-Mendelian.—Non-Mendelian inheritance may be of two types: (1) Biparental — in which the hybrid character is contributed by both male and female parents, and (2) Maternal — in which the character in question is controlled by the female parent only.

In variegated varieties of *Pelargonium zonale albomarginata*, *Antirrhinum majus albomaculata*, *Aquilegia vulgaris* (Baur, 1909, 1918) and *Oenothera* species (Stomps, 1917, cited by Scherz, 1927) there are plants in which some branches are solid white and some solid green in addition to periclinally variegated branches. Selfed flowers on these solid green and white branches produce progeny which are similar to their parent branch. But when flowers on the green and white branches are crossed reciprocally the hybrid seedlings are always "mosaic" (containing green and white sectors), regardless of the way the cross was made. The same phenomenon is repeated if flowers on solid green and white branches in any of the hybrid plants are crossed. Baur explained this on the basis that in these cases the cytoplasmic plastids, not the nucleus, was responsible for the hybrid character and that the cytoplasmic plastids were contributed by both the parents in these species. An almost similar situation has been found in variegated races of *Capsicum annum* (Ikeno, 1917).

The earliest case of maternal inheritance was described by Correns (1909) in *Mirabilis jalapa albomaculata*. Plants of this strain produced branches which had solid green or solid white leaves and also branches with variegated leaves. Selfed seedlings of completely green and white branches were green or white, respectively. Crosses between flowers on green and white branches always produced progeny which resembled the mother parent. No trace of any influence by the male parent was visible. Correns explained this maternal inheritance on the basis of cytoplasmic "disease" giving rise to the defective plastids in the albino parent. He assumed that the cytoplasmic contribution of the male parent was negligible and the zygote contained only the cytoplasm of the female parent. A similar situation was found by Baur (1910) in *Antirrhinum majus albomaculata* and *Aquilegia vulgaris* and also by Gregory (1915) in *Primula sinensis*. However, these workers thought that the "diseased" plastids themselves and not the "diseased" cytoplasm, were responsible for conveying the defective plastids from the mother to the progeny. According to these investigators, the young progeny of a branch with both kinds of plastids will give rise to variegated branches. This may be brought about by segregation of the plastids during somatic mitoses. Since these earlier reports, maternal inheritance of plastids has been found in a large number of species distributed in a number of genera and families (*Erodium cicutarium*—Scherz, 1927; *Zea mays*—Anderson, 1923; Rhoades, 1943; *Chlorophytum elatum* and *Chlorophytum comosum*—Collins, 1922; *Hydrangea*—Chittenden, 1926; *Arabis*, *Aubretia* and *Mesembryanthemum*—Correns, cited by Chittenden, 1926; *Stellaria media albomaculatus*, *Mercurialis annua*, *Senecio vulgaris*, *Taraxacum*

EXPLANATION OF FIGURES IN PLATE I

1. Stable clone of variegated *Chlorophytum elatum* form *medio-variegata*.
2. Unstable seedling clone of variegated *Chlorophytum elatum* producing pure green and albino shoots as well as variegated shoots. Generally the color of the flowering shoot resembles that of the central area of the leaf at its base. The bracts on the flowering shoot normally bear the same variegation pattern as is common in the leaves.
3. Albino and variegated (mutant) seedlings of *Chlorophytum elatum* from the selfed seeds of *medio-variegata* form.
4. Albino seedlings of *Impatiens sultanii* from the cross, variegated × green.

officinale, *Hieracium auricula*, *Urtica pilulifera*, and *Trifolium pratense*—cited by Scherz, 1927; *Hosta japonica*—Yasui, 1929; *Rhodeo japonica*, *Dendrobium* and *Habenaria*—Imai, 1935, from personal information from breeders, conclusions drawn probably from the results of selfing only; *Humulus*, *Pelargonium vars.* and *Melandrium album*—Sansome and Philp, 1939; *Triticum vulgare*—Umar, 1943; Pao and Li, 1946; Arnason, 1956; *Hordeum vulgare*—Arnason, Harrington and Friesen, 1946; Imai, 1928; *Sorghum* and *Phaseolus*—Snyder, 1951). In *Avena sativa*, Robb (cited by Ramiah *et al.*, 1935) reported an interesting case of maternal inheritance of variegation in which variegated plants had only striped progeny with occasional green plants but no albinos.

In certain cases inheritance of plastids may not be clear cut, for maternal plastid inheritance in these cases may be complicated by one or more accompanying phenomena such as gene segregation and plastid mutation (Imai, 1928; Rhoades, 1943).

MATERIALS AND METHODS

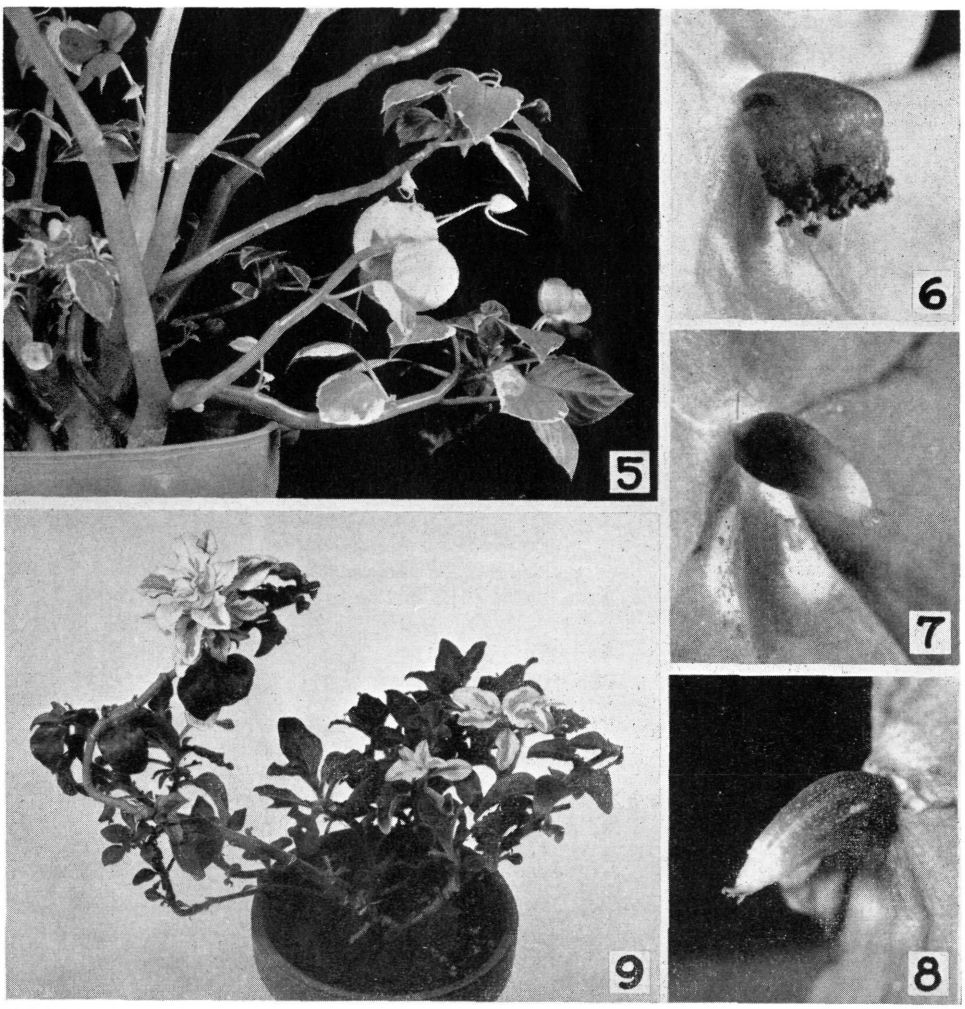
Impatiens sultanii.—Periclinally variegated plants of *Impatiens sultanii* have white bordered leaves. Histogenically, the L-II is albino (Pandey, unpublished). These plants also may bear branches which are albino (fig. 5). Flowers borne on the albino branches are cleistogamous and abscise before opening. Attempts to pollinate the flowers by cutting open well-developed flower buds failed to produce fruits. Therefore, flowers which appeared "normal" and were borne on the variegated branches were used for pollination.

In *I. sultanii*, natural self-pollination from the pollen of the same flower is impossible. At the time of anthesis, stigma is tightly capped by a fleshy androecium. The androecium dehisces from the groove in the outer surface of the cup, usually within 12 hours after flower opening and rarely before the flower is fully open (fig. 6). About 3 to 5 days after androecium dehiscence, the androecium cup dries and drops off, leaving the immature stigma exposed (fig. 7). Twenty-four to thirty-six hours elapse before the stigma is fully developed, open and receptive to pollen (fig. 8). Pollination before this stage of the flower is unfruitful.

Chlorophytum elatum.—Occasional variegated seedlings have been obtained from selfed variegated plants under greenhouse conditions (fig. 2). Comparatively stable *albo-marginata*, *medio-variegata* and *medio-albinata* forms (Imai, 1935) were easily obtained from these variegated plants. Generally the color of the flowering shoot resembles that of the central area of the leaf at its base. The bracts on the flowering shoot normally bear the same variegation pattern as is common in the leaves. Only stable forms of variegated plants (fig. 1) were used for cross pollination with pure green plants. Flowers were emasculated on the evening prior to flower opening. A description of various variegated plants used in this experiment is given in table 1.

Petunia violacea Lindl.—A single pink flowering plant of *Petunia violacea* having a variegated branch was found among a large group of normal green seedlings. The variegation in this branch was irregular and patchy (fig. 9). However, many flowers were available from solid or almost solid albino regions of the branch. A few flowers were also observed in which, out of 5 sepals, 2 or more were albino while the remaining ones were pure green or variegated.

P. violacea is a self-incompatible species (Mather, 1943). The flowers on pure green branches and the variegated branch of this plant were crossed reciprocally with another normal green, violet flowered plant. No emasculation in these flowers is necessary. However, only the flowers in which the shiny, receptive stigma was free from pollen, were chosen for cross-pollination. Anthers were removed from flowers before pollination.



EXPLANATION OF FIGURES IN PLATE II

5. Variegated plant of *Impatiens sultanii*. An albino shoot with cleistogamons flowers can be seen at the base of the stem.
6. The pistil of *Impatiens sultanii*. At the time of anthesis, stigma is tightly capped by a fleshy androecium. The androecium dehisces from the groove in the outer surface of the cup, usually within 12 hours after flower opening and rarely before the flower is fully open.
7. The pistil of *Impatiens suttanii* showing exposed immature stigma. About 3–5 days after androecium dehiscence, the androecium cup dries and drops off, leaving the immature stigma exposed.
8. The pistil of *Impatiens sultanii* showing mature stigma. Twenty-four to thirty-six hours after the dropping of the androecium cup the stigma is fully developed, open, and receptive to pollen.
9. Unstable plant of *Petunia violacea* giving rise to a few variegated shoots.

TABLE 1

Description of variegation in albo-marginata, medio-albinata *and* medio-variegata *forms of* Chlorophytum elatum

Plant No.	Plant Type (Form)	Description of variegation in leaves and flowering shoot
V	*Albo-marginata*	Fully green except for a narrow border which is yellow; flowering shoot green.
IX	*Albo-marginata*	Fully green except for a narrow border which is light green; flowering shoot green.
III	*Medio-albinata*	Center greenish yellow with light green streaks evenly distributed and border light green; flowering shoot yellow.
IV	*Medio-albinata*	Center yellow with few green streaks and border fully green; flowering shoot yellow.
X	*Medio-albinata*	Center yellowish green with few green streaks and border fully green; flowering shoot yellow (Reverse of Plant No. IX).
II	*Medio-variegata*	Center yellowish green with numerous greenish yellow streaks and border greenish yellow; flowering shoot yellowish green with many yellow streaks.
VIII	*Medio-variegata*	Center greenish yellow with fine green streaks as well as broad green stripes and border green; flowering shoot yellow with broad green stripes.
I	Normal green	Fully green, normal; flowering shoot green.
VI	Normal green	Light green, occasional yellowish green streaks in some leaves; flowering shoot green.
VII	Normal green	Light green, normal; flowering shoot green.

RESULTS

Impatiens sultanii.

Since variegated plants of this species are pollen sterile, only the result of one way cross, using the variegated plant as the female parent (variegated × green) is available (fig. 4). The color of the hybrid seedlings is as follows:

Cross	No. of seeds sown	No. of seedlings germinated		
		Albino	Green	Variegated
Variegated × green	83	26	0	0

The subepidemeral layer in this variegated plant has been found to contain only albino plastids. Thus, only plastids from the germinal tissue of the female parent are represented in hybrid seedlings.

Chlorophytum elatum.

Albo-marginata, *medio-variegata* and *medio-albinata* forms of this species were selfed, crossed reciprocally among themselves and some were also crossed reciprocally with normal pure green plants. Seeds obtained after selfing or crossing were

collected separately and sown separately for each capsule and the observations on the color of seedlings were recorded. The number of yellow, green or variegated seedlings obtained in various crosses are given in table 2.

It may be inferred from table 2 that the color of the progeny is almost entirely governed by the female parent (fig. 3). The progeny of plant IV which gives rise only to yellow seedlings, regardless of the type of cross, confirm this inference. The progeny of pure green forms are all green. *Albo-marginata* forms also produce

TABLE 2

Number of yellow, green or variegated seedlings obtained in various crosses of Chlorophytum elatum

Female Parent No.	Male Parent	No. of seeds sown	No. of seeds germinated	No. of Seedlings			Nature of Maternal Plastids	Percentage of seedlings with mutated plastids	
				Yellow	Green	Variegated			
II *Medio-variegata*	II	45	32	31	0	1	Yellow	3.1	16.9
	I	12	11	11	0	0		0	
	III	34	24	14	0	10		41.6	
	V	15	10	8	1	1		20	
III *Medio-albinata*	III	19	18	18	0	0	Yellow		0.0
	IV	12	12	12	0	0			
IV *Medio-albinata*	IV	95	69	69	0	0	Yellow		0.0
	III	15	15	15	0	0			
	VI	17	13	13	0	0			
	IX	30	26	26	0	0			
V *Albo-marginata*	V	16	15	0	15	0	Green	0	3.8
	IV	12	11	0	10	1		9	
VI Green	VI	26	16	0	16	0	Green		0.0
	IV	15	14	0	14	0			
VII Green	VII	11	11	0	11	0	Green		0.0
VIII *Medio-variegata*	VIII	19	15	3	6	6*	Yellow	80	39.5
	VII	12	12	12	0	0		0	
	IV	26	16	11	2**	3		31.2	
IX *Albo-marginata*	IX	39	22	0	22	0	Green	0	5.6
	IV	42	32	1	28	3		9.7	
X *Medio-albinata*	X	18	12	12	0	0	Yellow		0.0
	IX	38	22	22	0	0			

* Of these, three later became fully green.
** Both of these became variegated.

almost all green seedlings. The progeny of *medio-albinata* forms are all yellow. Most of the *medio-variegata* progeny are also yellow; however, there are some fully green or variegated seedlings. Thus, genetically there are three forms: 1) Pure green and *albo-marginata* which produce green seedlings, 2) *Medio-albinata* which produces yellow seedlings, and 3) *Medio-variegata* which produces mostly yellow seedlings with some green and variegated ones.

The mutation rate varies greatly from plant to plant. Most of the mutants arise in the progeny of *medio-variegata* forms. Also the mutation rates in the two

medio-variegata plants are obviously different. In *medio-albinata* and *albo-marginata* forms, the mutation rate is negligible. There are streaks on the leaves of *medio-variegata* forms which appear abruptly and are not connected with the base of the leaf. This indicates that such streaks are formed as the result of mutations in the early ontogeny of the leaf. If this is the case, it may be expected that such parents will have a high rate of mutation.

TABLE 3

Number and kinds of seedlings obtained from different crosses in Petunia violacea. *The plant with a variegated shoot had pink flowers. The variegated shoot had 3 variegated branches (Br. 1, Br. 2 and Br. 3). Pink flowers on variegated and green shoots were crossed reciprocally with violet flowers on a pure green plant. All flowers used from variegated branches had only albino sepals, unless otherwise stated*

Cross No.	Cross (♀ × ♂)	No. of Seeds Sown	No. of Seedlings Germinated		
			Albino	Green	Variegated
I Group	(August 5, 1956)				
(1)	Pink Var. Br. 1 × Violet Gr.	217	176	7	4*
(2)	Pink Var. Br. 1 × Violet Gr.	200	154	6	9*
II Group	(September 16–19, 1956)				
(3)	Pink Var. Br. 1 × Violet Gr.	279	154	0	0
(4)	Pink Var. Br. 2 × Violet Gr.	83	59	0	0
(5)	Pink Var. Br. 3 × Violet Gr. (All sepals greenish white)	260	159	0	0
(6)	Pink Var. Br. 3 × Violet Gr.	237	159	0	0
(7)	Pink Var. Br. 1 × Violet Gr. (2 sepals albino and 3 green)	195	0	182	0
(8)	Violet Gr. × Pink Var. Br. 2	365	0	232	0
(9)	Violet Gr. × Pink Var. Br. 2	315	0	210	0
(10)	Violet Gr. × Pink Gr.	324	0	280	0
(11)	Pink Gr. × Violet Gr.	252	0	120	0

*Out of four and nine variegated seedlings from crosses (1) and (2), one and eight seedlings, respectively showed variegation starting from the cotyledonary leaves; in the remaining seedlings, variegation appeared in later leaves.

In *medio-variegata* plant II there seems to be a tendency to produce more mutants in the progeny from the cross with plant III than by selfing. Conversely, in the cross with a different male parent (plant V) the mutation rate seems to have declined. In *medio-variegata* plant VIII, selfing produces a very high percentage of mutants (80%). In the cross with plant IV the percentage of mutants declines considerably (31.2%). In the cross with plant VII there are no mutants. These observations indicate that mutation rate in the zygote is affected by the male

parent. Apparently no plastids pass from the pollen to the zygote, as is evident from the cross in plant IV. It may be assumed that no male cytoplasm enters the egg at the time of fertilization. The influence of the male parent, therefore, must be exerted through the nuclear elements. The effect of the male parent appears to be different with the resultant different genetic constitution of the zygote.

Petunia violacea.

The single variegated shoot on the one plant gave rise to several small branches which bore flowers. Flowers on three of these branches, designated as Br. 1, Br. 2 and Br. 3, were used for cross pollination. Most of these flowers had nearly complete albino sepals, but a few of them had 2 or more entirely green or variegated sepals. Seeds of individual fruits were collected and sown separately.

Two sets of crosses were made about 45 days apart. The first group of crosses was made on August 5, 1956, and the other during the period September 16–19 as flowers opened. Mature fruits were harvested about a month after pollination in both crosses. The number and kinds of seedlings obtained from these crosses are given in table 3.

From group II crosses it is evident that seeds from flowers with all albino sepals gave rise only to albino seedlings when crossed with normal flowers on green shoots. Flowers on green shoots, when pollinated with pollen from flowers on variegated shoots, gave rise only to green seedlings. In cross (7) where the female flower had 2 albino sepals and 3 green, all resultant seedlings were green. Apparently the albino tissue did not include the germinal tissue from which the eggs arose.

It should be noted that no mutants arose from any cross in group II, whereas both crosses in group I resulted in some mutant progeny. However, 92.6 percent of the seedlings in group I crosses were albino. Some of the variegated seedlings had apparently green cotyledonary leaves but variegation appeared in later leaves.

DISCUSSION

The results of crosses between pure green and variegated chimeral plants in *Impatiens sultanii*, *Chlorophytum elatum* and *Petunia violacea* clearly suggest that plastid inheritance in these plants is strictly maternal. The cross between periclinally variegated and pure green plants in *I. sultanii* gave only albino seedlings. However, some of the reciprocal crosses between green and variegated plants of *C. elatum* and *P. violacea* gave rise to seedlings of maternal plastid color and also a few variegated and solid mutant (yellow or green) seedlings.

Collins (1922) reported maternal inheritance of plastids in *C. elatum* and *C. comosum* but he ascribed the appearance of variegation to "some peculiar action which brings about a somatic segregation of the two opposite characters and the disorderly distribution to leaves . . . upon the sequence and mode of subsequent meristematic segregation." Since Collin's hypothesis, we have come to a much better understanding of the origin and structure of chimeras and variegations. Many of the stable forms of variegation in *C. elatum* and other species are known to be periclinal chimeras and the relationship between their chimeral structure and hereditary behavior is easily understood.

There is a large difference in the percentage of mutants observed in the progeny of different plants. This indicates a genetical basis for the rate of plastid mutation. Most of the mutants in *C. elatum*, however, arose in the *medio-variegata* forms. There seemed to be a positive correlation between the number of streaks and stripes on the leaves and the number of mutant seedlings produced in their progeny. The two *medio-variegata* plants are periclinal chimeras; in plant II, the

first and second layers are yellow and the third layer green; and in plant VIII, the epidermis is green and the second and third layers yellow (Pandey, unpublished). As most of the broad stripes in the central region of the leaf in plant VIII seem to be connected with the epidermal layer which forms the border, it appears that stripes generally arise because of the occasional participation of the epidermis in the formation of deeper layers in the central area of the leaf. If it is presumed that mutant seedlings are produced because of the occasional replacement in the floral primordia, of the cells of histogenic layer L-II by the different kind of cells derived from the transverse division of the epidermal cells above, the increased number of mutant seedlings could be easily explained. On this hypothesis however, no variegated seedlings should appear in the progeny but only solid green or yellow. As variegated seedlings with variegated cotyledonary leaves do appear in the progeny, this hypothesis seems untenable.

There are many narrow streaks on the leaves which do not appear to be connected with the epidermal layer and which may have originated as mutations in color of the plastid in the early ontogeny of the leaf. It would have been easy to explain the occurrence of fine streaks as well as broad stripes on the leaves and the high number of mutants in the progeny on the basis of high rate of plastid mutation in these plants, but this does not fit with observations that: 1) broad stripes do not occur evenly in the entire leaf but are concentrated in the central area of the leaf and, 2) most of the broad stripes seem to be connected with the upper epidermal layer.

A high mutation rate of plastids combined with occasional replacements of the cells of the germinal layer by cells from the epidermal layer provide a most probable explanation for the appearance of a large number of mutant seedlings in the *medio-variegata* plants. The facts that the majority of the mutant seedlings (92.3%) in plant II, where there are only fine streaks but no broad stripes, are variegated and that plant VIII, which had broad stripes as well as fine streaks, produces variegated and also a number of solid green mutant seedlings support this hypothesis.

In *C. elatum*, the mutation rate of plastids in the zygote seems to be affected by the genetic constitution of the male parent. Ramiah *et al.* (1935) observed a higher percentage of chlorophyll defective seedlings in hybrid generations than in pure lines of rice.

In discussing maternal inheritance of leaf variegation in wheat, Arnson (1956) assumes that "since variegated plants have both normal and mutated plastids, it is possible that plastid segregation results in some eggs having only normal, some having mixed, and some only mutant plastids." This is difficult to accept since no one to date has clearly demonstrated two kinds of plastids in the same cell of a *mature* variegated plant. It is believed that the occurrence of variegated seedlings in the progeny of a plant showing maternal inheritance of plastids is due to the mutation of plastids in the egg or zygote. The segregation of two kinds of plastids into two distinct tissues takes place in the embryogeny of the seed. Upon selfiing a variegated plant, Arnason did not get any ablino seedlings but only green or variegated. This was explained by Arnason as being due to the high rate of back mutation from albino to green plastids. The same phenomenon may explain the result of Robb (1933, cited by Ramanujam *et al.*, 1935) in *Avena sativa*. He found maternal inheritance of variegation, with selfed seedlings of variegated plants giving rise only to striped progeny with occasional green plants but no albinos.

Winge (1919), after reviewing the literatue on variegated plants, presented a hypothesis in which he postulated that the physical basis of non-Mendelian inheritance might lie in plastids or cytoplasm. If it were in plastids, a variegated plant would produce albino, green or variegated progeny according to the kinds

of plastids present in the zygote; but if the physical basis for variegation was cytoplasm, all the progeny of a variegated plant would be variegated with no pure green or albino seedlings. In both cases the inheritance might be maternal or biparental according to whether or not in the particular species fertilization contributed the cytoplasm and plastids from the male parent. A large number of cases of maternal and some cases of biparental inheritance have been reported in which the physical transmission of individual kinds of plastids has been supposed to be the basis of the inheritance of variegation. Only two cases (*Capsicum*—biparental, Ikeno, 1917; *Humulus*—maternal, Winge, 1919) have been reported in which the physical basis of inheritance of variegation has been assumed to be the cytoplasm, and not the plastids. It is suggested that this behavior could also be explained on the basis of a high rate of reversible plastid mutation in the particular races of *Capsicum* and *Humulus*.

In the numerous reports of non-Mendelian inheritance it is a significant fact that with the exception of *Antirrhinum majus albo-maculata* and *Aquilegia vulgaris* (Baur, 1909, 1910 and 1918), the two types of hereditary transmissions, maternal and biparental, have not been found to occur in the same species (Randolph, 1922). This suggests that male cytoplasm enters the egg in some species and not in others. It is possible that in the strains of *A. majus* and *A. vulgaris* in which both maternal and biparental inheritance were reported there might be high rate of reversible plastid mutation resulting in each zygote containing both types of plastids. If this were true it might have easily confused the identity of maternal transmission of plastids.

In *Petunia violacea*, in the two crosses made between variegated and pure green plants in summer, some green or variegated mutants were produced but in the crosses made in early autumn no mutants were obtained in hundreds of seedlings. This indicates that mutation rate of plastids varies greatly with photoperiod, light intensity or temperature variations, or both of these. Ramiah *et. al.* (1935) also reported seasonal variation in the mutation rate in rice producing albino and other chlorophyll deficient mutants.

SUMMARY

A study of the inheritance of plastids in chimeral plants of *Impatiens sultanii* Hook. f., *Petunia violacea* Lindl. and *Chlorophytum elatum* R. Br. showed that plastid inheritance in these plants was strictly maternal.

In *I. sultanii* no mutant seedlings were observed in the progeny but in *C. elatum* and *P. violacea* some mutant seedlings were produced.

Different plants of *C. elatum* showed different rates of plastid mutation. However, most of the mutant seedlings were produced in the progeny of the *mediovariegata* plants. This has been explained to be due to (1) a high rate of plastid mutation in the cells and (2) occasional replacement of the cells of histogenic L-II by cells derived by transverse division from the epidermal cells.

In *C. elatum*, the mutation rate of plastids in the zygote seems to be affected by the genetic constitution of the male parent.

There is a strong indication that in *P. violacea* the mutation rate of plastids varies greatly with seasonal variation.

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